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Microhabitat Conditions Associated with the Distribution of Postdiapause Larvae of *Euphydryas editha quino* (Lepidoptera: Nymphalidae)

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ABSTRACT Microhabitats of postdiapause larvae of *Euphydryas editha quino* (Behr) were found to differ from random habitat points in percentage cover, grass, shade, shrub, and host plant (*Plantago erecta* E. Morris). Abundant host plant and little shade or overstory cover characterized larval microhabitat. Larvae found in shrub versus more open habitats occupied similar microhabitats but were significantly smaller, presumably because of delayed diapause break. Larval use of coastal sage scrub, when shrubs have been removed by disturbance (grading of dirt roads), suggests that some degree of intermediate disturbance resulting in removal of shrub canopy and increased insolation may benefit populations of this endangered insect.

KEY WORDS *Euphydryas editha quino*, endangered species, habitat, intermediate disturbance

Euphydryas editha (Boisduval) is a univoltine butterfly found in local populations over much of western North America (Howe 1975, Scott 1986, Parmesan 1996). Many subspecies have been described, including 12 from California (Garth and Tilden 1986). Although *E. editha* uses a wide range of hosts (mainly Scrophulariaceae and Plantaginaceae), local populations tend to be monophagous (White 1974, Scott 1986).

In coastal California, *E. editha* oviposits and feeds primarily on the annual plant *Plantago erecta* E. Morris (Ehrlich 1965, Singer 1972, Emmel and Emmel 1973, Orsak 1977, Ehrlich and Murphy 1981) (see Dempster in Hickman 1993 for plant taxonomy). Partially developed larvae undergo an obligatory summer diapause that is broken after fall and winter rainfall (Murphy and White 1984, Mattoni et al. 1997). Larvae then quickly complete their development and emerge as adults during the same spring (White 1974, Murphy and White 1984, Mattoni et al. 1997). Populations of *E. editha quino* (Behr) (= *E. editha wrighti* per Gunder), once distributed through much of lowland coastal southern California, have been declining since the late 1960s (Thorne 1970; Emmel and Emmel 1973; Orsak 1977, 1988; Mattoni et al. 1997). Populations and suitable habitat have been lost from urban and agricultural expansion (Thorne 1970, Emmel and Emmel 1973, Orsak 1988), and possibly by drought (Parmesan 1996), diskings, fire, and overgrazing (Orsak 1977). Currently, few populations of *E. e. quino* are known to exist, and on 16 January 1997, this subspecies received federal protection under the Endangered Species Act

(United States Federal Register, 16 January 1997). Knowledge of the microhabitat preferences of *E. e. quino* would be useful to conservation managers seeking to preserve populations of *E. e. quino*, or attempting to preserve or restore coastal sage scrub habitat with regard to arthropod community diversity.

Our primary objective with this research was to determine larval microhabitat use by comparing microhabitat conditions around individual larvae with conditions of similar areas uninhabited by larvae. Because shrub cover may affect solar incidence, perhaps affecting the rate of larval development, a secondary objective was to compare microhabitat conditions used by individual larvae found within coastal sage scrub with conditions used by larvae found on open ground without shrub overstory.

Materials and Methods

Study Site. This study was conducted at the southern end of the Southwestern Riverside County Multi-Species Reserve and associated Riverside County Parks Recreation Area ≈19 km south of Hemet, CA. *P. erecta* and associated *E. e. quino* populations were found through a grassland–coastal sage scrub vegetation mix dominated by *Eriogonum fasciculatum* Benth and *Artemisia californica* Less, or *Salvia mellifera* E. Greene. One *E. e. quino* population site was used in this study. The site was on a gentle west-facing slope dominated by *E. fasciculatum*–*A. californica* coastal sage scrub and annual grasslands. Grasslands were partially separated from the coastal sage scrub by an abandoned (for ≈10 yr) dirt road. Overall vegetative characteristics summarized by transect, and plant species collection data reflecting the coastal sage scrub portion of

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Table 1. Variables estimated for use in microhabitat description

Variable ^a	Possible effect on host biology	Possible effect on larval biology
<i>Plantago erecta</i>	Positive	Host required for larval existence
Forb	Negative	Reduced host availability, increased larval mortality, reduced oviposition site availability
Grass	Negative	High shade effect, reduced host availability, reduced larval mobility, reduced oviposition site availability
Shade	High shade: delay host senescence and development Low shade: increase rate of growth and senescence	High shade: Delayed emergence from diapause, reduced developmental rate, larval movement to areas of higher insolation Low shade: early emergence from diapause, accelerated developmental rate, larvae tend to remain in area
Shrub cover	(see Shade)	(see Shade)
Bare ground	Positive	Usually associated with high insolation, higher ambient temperatures, used for larval basking

^a Expressed as percentage cover; possible impacts of variables on larval and host biology are suggested.

habitat, are described elsewhere (see plot 2 of Osborne 1998).

Microhabitat Estimation. To determine larval microhabitat use, an area (60 by 160 m) encompassing the study area was searched for postdiapausing *E. e. quino* larvae. This area was searched on 5 occasions from November 1996 to 2 February 1997. Postdiapause larvae were first encountered on 10 January 1997. On 10 January 22, and 2 February, we systematically searched for larvae within strips of ground (2 m wide, 160 m long) across the study site. All searches were conducted between 1000 and 1400 hours (PST). Postdiapause *E. e. quino* larvae are easily observed by their heliothermic, black coloration (White and Singer 1987). All field work was conducted by K.H.O., who unequivocally identified all lepidopteran larvae.

On each date, the locations of all larvae encountered were flagged, as were locations of 30 points randomly selected from across the search area. Because of time constraints associated with microhabitat estimation, only 30 locations supporting larvae were randomly selected from the pool of all larvae found on each date (47 larvae on 10 January, 94 on 22 February, and 192 on 2 February). The random points represented microhabitat uninhabited by larvae and were located using an X-Y mapping coordinate system (± 1.0 m) placed over the entire study area.

On 2 February, locations of 30 larvae from an open area on the abandoned road (randomly selected from all those encountered) and 18 larvae found in dense sage scrub were used to compare larval microhabitat conditions between the 2 areas (open versus shrub-covered). Additionally, larval lengths (± 1.0 mm) were measured to determine if there was a difference in size between these 2 groups of larvae. Handling of these larvae to obtain biomass would have disrupted other research.

For each microhabitat point selected (larvae present or larvae absent), estimates of percentage cover by vegetation and shade were taken at each date on which larvae were encountered. These estimates were taken within 24 h after locations were flagged and selected. Data were collected using a Daubenmire quadrat (0.5 m by 0.25 m) (Daubenmire 1959) from a 0.78-m² area (0.5-m radius) placed around each point. Four quadrat estimates of vegetation were taken

around each point (larvae present [$n = 30$ for each date], larvae absent [$n = 30$ for same dates], and larvae in scrub cover [$n = 18$] versus larvae on dirt road [$n = 30$]). The mean of the 4 estimates for each point was used in all analyses. Vegetation categories measured were *P. erecta*, total forbs [usually including *Erodium cicutarium* (L.), *Uropappus* (= *Microseris*) *lindleyi* (deCandolle), *Lactuca serriola* L., and *Lepidium nitidum* Torrey & Gray], total grasses [usually *Bromus madritensis* L., *Avena fatua* L., and *Schismus barbatus* (L.)], and total shrubs. *Bare ground* was defined as soil surface not covered by live vascular plants; soil surface covered by cryptogamic crust (algae, lichen, or moss) or leaf litter was considered as bare ground. Shade was estimated as percentage ground surface obscured from direct overhead view by vegetation; ground obscured by vegetation <3 cm in height was not considered as shaded.

When estimating microhabitat conditions of larvae in sage scrub versus larvae encountered in the open, shrub cover was measured with 2 perpendicular 2-m line transects centered at each point. Here shrub cover was estimated (± 10 cm) along the line transects extending 1 m in radius out from the point. This additional estimate of shrub cover was taken to determine at what spatial scale larvae discriminate shrub cover. Shade was estimated along each transect line as above. Table 1 lists microhabitat variables measured and suggests possible impacts each has on biology of larvae and host.

Analysis. Microhabitat data were combined by category (larva present versus larva absent) across the 3 collection dates (10 and 22 January, 2 February), $n = 30$ from each category date combination yielding 90 microhabitat estimates per category. Data were transformed by arcsine square-root to meet assumptions of normality. Hotelling's T^2 -test was used to test for microhabitat differences between locations in which larvae were present versus locations in which larvae were absent. The Wilks γ approximation of F was used to determine significance (Litell et al. 1991). Given a significant Hotelling's T^2 -test, absolute values of univariate t -values were compared with $t_{crit} = 4.25$ at $\alpha = 0.01$ and $t_{crit} = 3.65$ at $\alpha = 0.05$ to determine significant differences between individual microhabitat estimates (Harris 1995). The value t_{crit} is an adjusted t

Table 2. Mean (\pm SEM) microhabitat conditions associated with presence or absence *E. e. quino*

Microhabitat condition (% cover)	Larva present (<i>n</i> = 90)		Larva absent (<i>n</i> = 90)		df	<i>t</i>	<i>P</i> > <i>t</i>
	Mean	(\pm SEM)	Mean	(\pm SEM)			
Bare Ground	70.80	(1.54)	39.19	(2.42)	178	10.232 ^a	<0.0001
Grass	11.78	(1.44)	35.53	(2.16)	178	-9.186 ^a	<0.0001
Shade	5.8	(0.81)	31.54	(2.94)	178	-9.096 ^a	<0.0001
<i>P. erecta</i>	1.18	(0.18)	0.28	(0.08)	178	8.481 ^a	<0.0001
Shrub	3.69	(0.06)	19.78	(2.79)	178	-5.666 ^a	<0.0001
Forb	18.23	(1.11)	17.12	(1.47)	178	1.401	0.160

^a Significant at $\alpha = 0.01$ ($t_{crit.} = 4.25$). One *Plantago* plant $\approx 0.25\%$ cover.

derived as $214 \sqrt{T^2_{crit.}}$, compensating for experiment-wise error (Harris 1995).

To compare microhabitats used by larvae in coastal sage scrub versus larvae found in the more open habitat, microhabitat data were transformed and analyzed as above (here $t_{crit.} = 4.71$ at $\alpha = 0.01$ and $t_{crit.} = 3.97$ at $\alpha = 0.05$). Differences in the shrub cover estimated by transect, and larval length were analyzed with univariate *t*-tests (and these latter data were not included in the Hotelling T^2 analysis).

Results

General Observations. Postdiapause larvae were not seen on searches during November through 20 December 1996, but appeared by 10 January 1997. Effectiveness of search in heavy ground cover was demonstrated by location of many small, dark colored *Kodiosoma fulva* Stretch, *Arachnis picta* Packard, and *Gramia nevadensis* (Grote) larvae (all Arctiidae). Larvae that had emerged from diapause were ≈ 1 cm long, and often found in clusters of several per square meter at margins of dense grass and shrub cover. From 10 January through 2 February 1997, numbers of postdiapause larvae increased; clusters of larvae (mostly located along the abandoned road) gradually dispersed over much of the study area. On 22 January, postdiapause larvae (≈ 1 cm long) began to appear in a patch of dense coastal sage scrub separated from the main group of larvae by ≈ 40 m. By 2 February, nearly all larvae on the abandoned road had developed to the last instar, whereas most of those in the dense coastal sage were in the preultimate or earlier instars. Larvae

were present only where *P. erecta* occurred at densities of >1 plant per square meter. Foraging larvae left a meandering trail of defoliated host plants ringed with frass. Most larvae, on all sample dates, were found along the abandoned road and adjacent trail.

Microhabitat Use by Larvae. Significant differences in microhabitat conditions were found between areas with larvae versus areas without larvae (Hotelling $T^2 = 140.86$; $\gamma = 0.560$; $F = 22.69$; $df = 6, 173$; $P < 0.0001$). *Plantago erecta* and bare ground were significantly more abundant in areas occupied by larvae (Table 2). Areas with larvae also had significantly lower vegetative cover, height, and shade than areas in which larvae were absent (Table 2).

Microhabitat conditions associated with larvae found in dense coastal sage scrub differed significantly from conditions associated with larvae found outside of the scrub habitat in more open areas (Hotelling $T^2 = 207.16$; $\gamma = 0.185$; $F = 30.12$; $df = 6, 41$; $P < 0.0001$). Larvae in coastal sage scrub always were encountered in areas between shrubs. Although these 2 habitats (open versus shrubby) differed significantly with respect to shrub cover at the 1-m scale, shrub cover did not differ at the 0.5-m scale (Table 3). Additionally, cover by *P. erecta* did not differ between scrub versus open areas. Larvae occurring in sage scrub were significantly smaller than larvae on the abandoned road ($t = -6.306$, $P < 0.0001$; Table 3).

Discussion

Our results (Table 2) agree with other observations that host plant abundance is associated positively with

Table 3. Mean (\pm SEM) and range for larval length and microhabitat conditions associated with *E. e. quino* larvae in coastal sage scrub and larvae from abandoned road on 2 February 1997

Variable estimated	Larvae in coastal sage scrub			Larvae in open habitat			df	<i>t</i>
	Range	Mean	(\pm SEM)	Range	Mean	(\pm SEM)		
Larval length, mm	8-23	15.61	(1.14)	15-30	23.57	(0.70)	46	-6.306***
% shrub cover to 1-m radius	2-36	14.39	(1.97)	0-20	2.70	(0.91)	46	7.007***
% forb cover	0-25	12.67	(2.52)	25-50	42.50	(2.13)	46	-8.426**
% shade cover	0-50	10.28	(2.90)	0-10	1.20	(0.52)	46	5.070**
% grass cover	0-75	23.61	(5.77)	5-50	10.62	(5.62)	46	4.691*
% shrub cover to 0.5-m radius	0-50	6.39	(3.20)	0-10	0.33	(0.33)	46	2.630
% <i>P. erecta</i> cover	0-10	1.58	(0.60)	0.25-5	1.17	(0.24)	46	-0.013
% bare ground	10-75	56.11	(5.24)	25-75	55.83	(2.30)	46	0.011

***, significant at $\alpha = 0.01$ (unadjusted $t_{crit.} < 2.70$); **, significant at $\alpha = 0.01$ ($t_{crit.} = 4.71$); *, significant at $\alpha = 0.05$ ($t_{crit.} = 3.97$). One *Plantago* plant $\approx 0.25\%$ cover.

habitat use by *E. e. quino* (Orsak 1977, 1988; Murphy and White 1984). Additionally, nonhost plants, especially Eurasian exotics (*Bromus*, *Avena*, *Schismus*, *Erodium*, and *Lactuca*), may indirectly affect *E. e. quino* distribution through competitive exclusion of host plants (Table 2) (McNaughton 1968, Proctor and Woodwell 1975, Murphy and Ehrlich 1988, Murphy and Weiss 1988, Mattoni et al. 1997).

Diapausing *E. e. quino* larvae, not found in this study, must have been abundant during the early weeks of our field work. Larvae are believed to diapause in soil, leaf litter, or under rocks. Location of diapausing *E. e. quino* larvae in the field is undocumented but given speculatively by Mattoni et al. (1997). The presence of clusters of diapause-breaking larvae found near dense grass and shrub cover suggests larva may diapause within or under these materials.

The biology of *Euphydryas editha editha* (Boisduval) (= *E. e. bayensis* per Sternitzky), is closely linked to its host phenology. Successful *E. e. editha* postdiapause larval development, adult oviposition, and subsequent prediapause larval development through at least 3rd instar, must precede the *P. erecta* host senescence (Singer 1972, Ehrlich et al. 1980, Ehrlich and Murphy 1981, Dobkin et al. 1987, Weiss et al. 1988). Host plant germination and senescence are, in turn, affected by both solar insolation and the timing and abundance of rainfall (Murphy and White 1984, Dobkin et al. 1987). To complete development before host senescence, postdiapause *E. e. editha* larvae seek microclimates with high solar insolation (Weiss et al. 1987), where basking increases the rate of larval development (White 1974, Weiss et al. 1988). Our finding that *E. e. quino* larvae are found in microhabitats characterized by high solar insolation is consistent with these findings for *E. e. editha*. Postdiapause *E. e. quino* larvae select microhabitat sites with low shade cover, and thus areas with reduced shrub and grass coverage. Nonhost plants appear to reduce larval microhabitat quality by screening solar insolation. In the *E. e. editha* system, low solar incidence on north-facing slopes was associated with slower growth rates and a delayed emergence from diapause (Weiss et al. 1987). In our study, the effects of shade may explain the delayed emergence from diapause (a developmental delay) of larvae found in areas dominated by shrubs. Although not documented, larvae in coastal sage scrub may maximize solar insolation by using the open areas between shrubs on a spatial scale of <1 m; indeed, larvae in dense shrub areas are found between, rather than under, individual shrub canopies.

In serpentine grasslands (relatively devoid of shrubs), topographic heterogeneity with respect to slope exposures is thought to contribute to the long-term population stability for *E. e. editha* (Dobkin et al. 1987, Weiss et al. 1988). Solar insolation varies from the maximum on south-facing slopes where *P. erecta* may develop and senesce early in the season (and larvae develop faster) to the more shaded northerly slopes where plants persist longer (and larval development occurs more slowly). During drought, northerly slopes afford more persistent host resources for

developing larvae and adult oviposition (Weiss et al. 1988). In coastal sage scrub and chaparral, insolation may vary greatly over <1 m, from shade under a shrub to fully exposed ground between shrubs or over a few meters between north and south sides of shrub patches. Shrub-generated microclimatic heterogeneity superimposed over topographic habitat heterogeneity in coastal sage scrub and chaparral may provide additional long-term population stability to some *E. e. quino* populations by increasing small-scale spatial variation in host plant phenology and developmental rates of larvae.

Finally, the use of disturbed habitat (abandoned dirt road) by *E. e. quino* suggests that some degree of intermediate disturbance (Connell 1978) may benefit populations of this butterfly. In this study, previous disturbance (e.g., grading of roads) appears to have created areas characterized by fewer shrubs, less overall vegetation cover and shade, and more host plants than undisturbed adjacent areas. These disturbed areas, with abundant *P. erecta*, appear to be favored by *E. e. quino* postdiapause larvae. Given the current restricted distribution and endangered status of this butterfly, well-planned management of previously disturbed habitats, combined with preservation and restoration of coastal sage scrub habitat, may lead to restoration of this subspecies. Additional studies are needed on the effects of disturbance on the suitability of habitat for *E. e. quino*.

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